

laboratory, however, phenotypic variation among groups remains high even with large numbers of initial colonists. And when groups are selected on the basis of their phenotypic properties, there is typically a response to selection (Goodnight & Stevens 1997). The theoretical models with their simplifying assumptions got it wrong. Theoretical models that assume more complex interactions do a better job (e.g., Bijma & Wade 2008; Gilpin 1975; Goodnight 2011; Wilson 1992).

These conclusions apply to social insect colonies, as well as to other groups. One of my few disagreements with Smaldino is that he endorses the formulaic statement that eusociality in insects can be explained by high genetic relatedness or as “the extended phenotype” of the queen. High genetic relatedness contributes to heritable phenotypic variation among groups, but the colony is the unit of selection, and the proximate mechanisms that evolve are highly distributed among individuals. It is hard to imagine the cavity selection process of honeybee swarms as the extended phenotype of the queen when the queen plays no role whatsoever (Seeley 2010).

I do agree with Smaldino’s points about equivalence. It is important to establish the equivalence of multilevel selection theory and inclusive fitness theory for models of individual-level traits, so that they are not pointlessly argued against each other. The more individuals become part of a complex distributed system with a group-level adaptive function, however, the more difficult it becomes to imagine them as optimizing units.

To summarize, whenever selection operates at a given level of a multitier hierarchy, units at that level should become the object of functional analysis, and units at lower levels should be studied as proximate mechanisms. This intuition already exists for the study of genes in individuals, when individuals are the unit of selection. It is only beginning to be applied for the study of individuals in groups, when groups are the unit of selection. Smaldino’s target article is an important step in this direction with an emphasis on human cultural evolution, but the same algorithm applies to all multilevel evolutionary processes.

## Many important group-level traits are institutions

doi:10.1017/S0140525X13003087

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**Abstract:** Smaldino makes a solid contribution to the literature on the evolution of human social organization by pointing out that group-level traits (GLTs) often emerge from the interactions of group members in such a way that their effects are not easily partitioned into individual selection. However, we argue that he too readily dismisses institutional analysis as a tool for understanding these traits.

We largely support the main argument of Smaldino’s article and think his ideas about GLTs will be useful for understanding the evolution and origin of complex organizations and societies. We especially welcome the insight that many important GLTs are emergent properties that may be difficult, or even impossible, to partition into units of individual selection. However, we also think Smaldino is too quick to dismiss existing institutional frameworks as useful ways to think about GLTs.

In multilevel selection (MLS) models of cultural evolution, the fitness consequences of traits are partitioned between at least two components, typically group-level and individual-level

components (Henrich 2004a). For example, if groups of agents play public goods games, the group benefits of the public good may be accounted for in between-group fitness, and the individual costs may be accounted for in within-group fitness. The typical argument against MLS accounting is that partitioning at the group level can be unnecessary because selection can often be more parsimoniously accounted for at the individual level. However, Smaldino takes the opposite track, arguing that group traits are emergent and, by definition, not easily reduced to aggregates of individual-level traits.

Although we agree with the broad strokes of Smaldino’s thesis, we think he errs in denying that many of these GLTs can be usefully classified as “institutions” and studied using existing tools of institutional analysis (e.g., North 1990). Institutions are often defined as the “rules” that are the properties of groups called “organizations.” Institutions range from informal norm-based rules to formally codified laws of complex societies, and a key feature of institutions is that they are often maintained by systems of rewards and punishments that suppress individual-level deviation and stabilize behavior at a game theoretic equilibrium. Because the space of stable institutions is vast in both theory and in practice, institutional change can often be appropriately modeled as between-group “equilibrium selection” (Boyd & Richerson 1990). In fact, it is relatively common for institutional economists and political scientists to treat formal institutions, such as the rules of political and economic organizations, as group-level traits in direct evolutionary competition. This is the sort of simplification to group-level traits for which Smaldino seems to advocate.

“Constitutional democracy” is a good example of an institutional GLT that can spread between countries as a result of selection-like processes (Cederman & Gleditsch 2004). However, breaking something as complicated as the rules governing a constitutional democracy down to units of individual-level selection seems prohibitively difficult – a constitutional democracy is more than just the aggregate sum of individual-level costs and benefits. In short, it is emergent.

Smaldino gives three examples of where he does not consider institutions to qualify as group level traits:

Group-level traits are related, but not equivalent to institutions... a group-level trait is the *phenotypic effect* of social organization. Thus, examples of group-level traits are the music rather than the rock band, the election of a leader who reflects the public interest rather than the democratic voting system, the sailing ship’s voyage rather than the crew positions, the economic surplus rather than the market economy. (sect. 2, para. 2)

We disagree with Smaldino and think that an institutional framework is more useful for understanding the spread of GLTs than a focus on phenotypic effect.

Taking Smaldino’s suggestion that a GLT should be considered the “economic surplus rather than the market economy” (sect. 2, para. 2), one might ask how does economic surplus spread? Does a poorer country look to a richer country and say “we should copy their economic surplus?” That probably would not get them very far. Instead, a country might more successfully emulate the economic or political institutions that may underlie another country’s economic surplus. We might therefore think of “economic surplus” as an indication of the success of the GLT, not the trait itself.

Taking Smaldino’s other examples; a country is more likely to emulate a successful country’s political institutions than it is to elect their political leaders. Similarly, during the Meiji restoration, the Japanese slavishly emulated British naval institutions, including standard crew positions (Goldman 2002). However, they did not attempt to recreate particularly successful British voyages.

Although the institutional framework is more useful than Smaldino supposes, not all GLTs need be institutions. A lot of bands emulated the music of the Beatles, for example. However, although the sound of a Beatles’ song can be emulated directly,

it is most efficient to do it with the same numbers and types of musicians. Some styles of music have an institution-like structure enforced by fans. Fans can usually tell you their favorite style of music—classical, country and western, folk, rhythm and blues, rock, etc. Musicians who change styles may lose all or part of their audience when they do so.

In summary, we think Smaldino's article highlights a future direction for modeling the evolution of social complexity and institutional selection. He convincingly argues that GLTs are useful simplifying concepts. We hope his insights will be integrated into the study of both simple and complex emergent institutions.

## Author's Response

### Group-level traits emerge

doi:10.1017/S0140525X13003531

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**Abstract:** Most commentators supported the thesis of the target article, though there were also those who were less fully persuaded. I will begin with a response to the most critical commentaries. First, I will justify an evolutionary perspective that includes group organization and nongenetic inheritance. Next, I will discuss the concept of emergence. Following that, I will transition to an exploration of ideas and concerns brought up by some of the more supportive commentators. This will include a discussion of different types of groups; the psychology of group-level traits; the uses and limitations of an institutional perspective; the link between transmission, adaptation, and selection; current and future methodologies; and the variety of fields that may benefit from a group-level traits perspective.

I am grateful to all the commentators and humbled by the variety of responses and the care that went into them. Thankfully, the majority of commentators are on board with the basic thesis of the target article: that group-level traits are distinct from individual-level traits and constitute different units of analysis in evolutionary thinking. As such, a large part of this response will entail clarifying and extending the idea of group-level traits in response to various suggestions and concerns brought up by the commentators.

Although most commentators supported the thesis of the article, there were also those who were not so readily persuaded that any new perspectives or methods are necessary to understand the evolution of human social complexity. Some of these commentaries expressed concerns over ideas that were at the foundation of my argument. I believe it is crucial for any discussion to have a firm foundation. Therefore, I will begin with a response to some of the most critical commentaries. First, I will justify an evolutionary perspective that includes group organization and nongenetic inheritance. Next, I will discuss the concept of emergence and how I use it to elucidate group-level properties and behaviors.

Following that, I will transition to an exploration of a number of important ideas and concerns brought up by some of my more supportive commentators, as well as by

those who accept the basic thesis but were critical of some of the details. This will include a discussion of differences among types of groups; the psychology of group-level traits; the uses and limitations of an institutional perspective; the link between transmission, adaptation, and selection in the evolution of group-level traits; current and future methodologies for the study of social behavior and evolution; and the various fields in the biological and social sciences that may benefit from a group-level traits perspective.

### R1. The false allure of “standard evolutionary theory”

The most severe critique of the target article comes from **Scott-Phillips & Dickins**, who claim there is no need whatsoever for new methods for understanding group-level traits. Their attack is not, in fact, leveled explicitly at the group-level traits idea but is a larger attack on recent advances in evolutionary theory that incorporate methods of nongenetic inheritance; these include cultural evolution, epigenetic inheritance, and niche construction. They argue that these approaches are misguided and represent disruptive deviations from the path to an enlightened understanding of evolution, one that focuses on those methods that they view as constituting “standard evolutionary theory.” As this is a critique on the overarching framework essential to the approach presented in my target article, it is important to address their comments first.

**Scott-Phillips & Dickins's** critique stems from two beliefs: (1) that all heritable traits, including behaviors, are derived from genes (e.g., Dickins & Rahman 2012), and (2) that culture is a strictly proximate mechanism. Neither belief withstands closer examination. First, a gene-only view of evolution ignores the role of self-organizing forces in shaping traits (Kauffman 1993) and the fact that nongenetic phenotypic factors may be both heritable and subject to natural selection, including epigenetic markers (Jablonka & Lamb 2005), environmental niches (Odling-Smee et al. 2003), and cultural institutions (Richerson & Boyd 2005). Second, treating culture as a proximate mechanism ignores both the coevolutionary interaction between culture and genes and the fact that culture itself evolves in a Darwinian process (Mesoudi 2011). Scott-Phillips & Dickins also seem confused about basic principles of multilevel selection theory. For example, they argue against the use of multilevel selection (MLS) theory by saying “there is no formal justification to consider the cultural group as a unit of selection.” But MLS theory does not, in fact, require that the group is a unit of selection, only that the circumstance of belonging to a group influences individual fitness (Okasha 2006). Finally, Scott-Phillips & Dickins take me to task for ignoring the work of cultural epidemiologists such as Dan Sperber. I agree that cultural epidemiological models are valuable, but their direct relevance to a conceptual discussion of group-level traits is minimal. Further, the cultural evolutionary perspective promoted by Boyd, Richerson, and colleagues (Boyd & Richerson 1985; Richerson & Boyd 2005; Mesoudi 2011) is completely coherent with cultural epidemiological models (Henrich et al. 2008), and because these models also treat cultural variants as individual-level traits, the discussion in the target article applies to them as well.